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**Noise affects resource assessment in an invertebrate**

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Anthropogenic noise is a global pollutant, affecting animals across taxa. However, how noise pollution affects resource acquisition is unknown. Hermit crabs (*Pagurus bernhardus*) engage in detailed assessment and decision-making when selecting a critical resource, their shell; this is crucial as individuals in poor shells suffer lower reproductive success and higher mortality. We experimentally exposed hermit crabs to anthropogenic noise during shell selection. When exposed to noise, crabs approached the shell faster, spent less time investigating it, and entered it faster. Our results demonstrate that changes in the acoustic environment affect the behaviour of hermit crabs by modifying the selection process of a vital resource. This is all the more remarkable given that the known cues used in shell selection involve chemical, visual and tactile sensory channels. Thus, our study provides rare evidence for a cross-modal impact of noise pollution.

## 1. Introduction

Anthropogenic noise is omnipresent in both aquatic and terrestrial habitats and has become a global pollutant affecting species across the phylogenetic tree (e.g. [1, 2]). However, our understanding of how novel selection pressures, such as anthropogenic noise, affect animals' ability to assess vital resources is unknown.

Across the animal kingdom, the assessment of resources, such as territories, mates and food, is of critical importance, with cues used that correlate with expected gains in fitness, and result in adaptive motivational change [3, 4]. Human-induced environmental changes may affect the ability of individuals to gather all the information necessary to assess vital resources.

Hermit crabs engage in a complex assessment process when selecting a vital resource, their shell, which provides protection from predators, desiccation, and extremes of salinity [5]. The assessment crabs carry out on shells involves information-processing and decision-making, occurring in discrete stages [6]. Thus, relevant information must be filtered from the environment, a process known as attention [7]. Shell selection requires sustained attention to make a decision, as the quality of the chosen shell has direct fitness consequences for the individual [6, 8]. If species rely on perceiving information to assess vital resources, changes in the acoustic environment through noise pollution could have far-reaching consequences by affecting fitness-relevant information gathering and decision-making.

Here we test whether anthropogenic noise affects the acquisition of a vital resource. Noise pollution research has focused primarily on species that use acoustic signals. However, there is some evidence that invertebrates that do not rely on acoustic signals are also affected by noise [9]. Sound consists of two components: particle motion and sound pressure, both of which can provide information to individuals [10]. Decapods, such as hermit crabs, appear to perceive particle motion only, but are capable of perceiving sound within the range of those produced by anthropogenic activities [11, 12]. Using playback experiments, we manipulated the acoustic environment of hermit crabs by exposing them to either anthropogenic noise, or a control during shell selection. We predicted that individuals exposed to noise would adjust their assessment and decision-making processes in response to changes in the acoustic environment.

## 2. Material and methods

Hermit crabs (*P. bernhardus*) were collected from rock pools and removed from their shells using a bench-vice (for details see electronic supplementary material). To ensure standardised high levels of motivation for shell acquisition, we provided individuals with a non-preferred *Gibbula cineraria* shell, 50% the weight of each individual's relative ideal shell weight [5].

To create different acoustic environments, the experiment consisted of one of two 30 minute treatments: anthropogenic noise, or a control (for details see electronic supplementary material and Figure S1). A crystallising dish, 17cm in diameter, was used as an arena. Before each trial the arena was filled with fresh, 12°C seawater to a depth of 7.5cm. Crabs were randomly assigned to either the control (N=31), or the noise (N=33) treatment. Each subject's

ideal shell of relatively preferred weight and species (*Littorina obtusata*) [5] was placed on one randomly allocated side of the arena and the focal individual on the other.

To allow crabs to recover from handling, they were held within an upturned glass container for 5 minutes prior to the start of the treatment, following which the glass was removed, the playback started, and the trial began. A trial ended when an individual moved away either in the new 100% shell, or having rejected it, and remained in the 50% shell [3]. If crabs did not investigate the shell, or make a decision, the trial was ended after 30 minutes. We measured the following response variables: (i) latency to contact shell (sec), (ii) investigation (sec), i.e. time shell is investigated before abandoning 50% shell and entering 100%, or aborting further shell investigation, (iii) latency to enter shell (sec), i.e. total time from the start of the experiment to leaving the 50% shell, (iv) final decision (yes/no), i.e. reject or accept 100% shell, and (v) latency to final decision (sec). In four cases crabs did not investigate the offered 100% shell within 30 minutes [3, 13] and were thus excluded from further analysis.

Since data did not fulfil the assumptions of parametric tests we used Mann-Whitney U tests throughout, unless stated otherwise. 64 individuals were included in all analyses, with the exception of ‘latency to enter shell’, where 10 individuals who did not enter the presented 100% shell could not be included. All analyses were carried out in RStudio 0.99 [14]; data is available as electronic supplementary material.

### 3. Results

Latency to shell contact was shorter during noise than in the control exposure ( $N_{\text{Noise}}=33$ ,  $N_{\text{Control}}=31$ ,  $U = 749$ ,  $p = < 0.001$ ; figure 1a). Crabs exposed to noise also spent less time investigating shells than those exposed to the silent control ( $N_{\text{Noise}}=33$ ,  $N_{\text{Control}}=31$ ,  $U = 710$ ,  $p = 0.0076$ ; figure 1b). The time it took crabs to enter the preferred shell was shorter during noise than during the control playback ( $N_{\text{Noise}}=25$ ,  $N_{\text{Control}}=29$ ,  $U = 530$ ,  $p = 0.0036$ ; figure 1c). Latency to final decision was shorter during the noise than during the control playback ( $N_{\text{Noise}}=33$ ,  $N_{\text{Control}}=31$ ,  $U = 730$ ,  $p = 0.003$ ; figure 1d). Out of the 31 crabs in the control treatment, 28 took the optimal shell, i.e. making the ‘correct’ choice, whereas out of the 33 crabs in the noise treatment, only 24 took the optimal shell (Chi-square test:  $\chi^2=3.248$ ,  $p=0.071$ ).

#### 4. Discussion

Our results demonstrate that anthropogenic noise alters an animal’s assessment of a vital resource. Contrary to predictions, experimental exposure to noise did not extend the assessment of a shell, but instead shortened it for all measured variables. When exposed to noise crabs approached the shell faster, spent less time investigating it, and entered it faster. Thus, the changed acoustic environment had a clear effect on the behaviour of hermit crabs.

It is interesting to note that noise affected hermit crabs across sensory modalities, thus our study provides rare evidence for a cross-modal impact of noise pollution [9, 15]. Hermit crabs use chemical, visual and tactile information to assess shells [5, 16, 17]. As changes in the acoustic environment do not affect any of these sensory modalities directly, it is unlikely

that the differences in behaviour between the two treatments result from direct influences on these sensory channels.

There are several non-mutually exclusive hypotheses regarding how noise may affect assessment and thereby shorten the shell selection process: noise may affect cognitive processing [18], cause stress [19], and/or mask sound [20], all of which could affect shell selection simultaneously. However, as an empty gastropod shell does not emit sound per se, masking by noise would likely have no effect on shell selection. In contrast, changes in the acoustic environment may affect attention, as individuals can only process a finite amount of information simultaneously [21].

During the assessment of a new shell, individuals have to divide their attention between at least two different processes: the assessment of the shell and vigilance for potential predators, as individuals are highly vulnerable during shell exchange [5]. Thus, a novel stimulus such as noise may force individuals to reallocate their attention [22]. Such reallocation of an individuals' finite attention has been demonstrated in Caribbean hermit crabs when responding to an approaching threat [23]. Our results are also consistent with noise increasing motivation [8] to gain the resource. For example, individuals may be interpreting noise as a threatening stimulus, such as a predation [24], increasing their motivation to gain a shell offering increased protection.

Generally, care must be taken when extrapolating results from short-term tank-based experiments to meaningful implications for individuals living in the wild, because underwater



acoustics are complex (e.g. [25, 26]) and noise levels in tanks may be higher than those experienced in nature. However, experimental studies in a controlled environment provide a starting point to examine effects of anthropogenic noise, which have only recently been acknowledged, paving the way for future studies in real world scenarios. Moreover, in the marine environment noise is often chronic [27] and it remains to be investigated whether species can habituate and become tolerant to repeated, or chronic noise exposure. More broadly, theoretical simulations have demonstrated that noise does not necessarily impair information assessment [28] and could offer a source of public information for eavesdroppers [29]. Responses to anthropogenic noise are complex [24], depending on the biology of the species. The extent to which these responses impact fitness, either positively or negatively, remains to be understood.

In conclusion, our study provides evidence that changes in the acoustic environment affect the acquisition of a fitness determining resource, as survival, growth, and reproduction of hermit crabs depend on the occupancy of shells of appropriate size and shape (e.g. [30]). Notably, despite the known cues used in shell selection not being directly affected by changes in the acoustic environment, noise still affects a fitness-relevant process, offering an example of a cross-modal impact. Moreover, this work contributes to the small, but increasing body of evidence that it is not only vertebrates which are affected by noise, but also invertebrates [31].

Ethics. There are no legal requirements for studies involving decapod crustaceans in the United Kingdom and Northern Ireland, but we followed the Association for the Study of Animal Behaviour Guidelines for the Use of Animals in Research.

169 Data accessibility. Data are available at Dryad Digital Repository, DOI: 10.5061/dryad.g1hk2  
170 [32].

171 Authors' contributions. E.W., G. A. and H.K. conceived and designed the study, E. W.  
172 collected the data, all authors analysed the data and wrote the manuscript. All authors gave  
173 final approval for publication and agree to be accountable for all aspects of the work in  
174 ensuring that questions related to the accuracy or integrity of any part of the work are  
175 appropriately investigated and resolved.

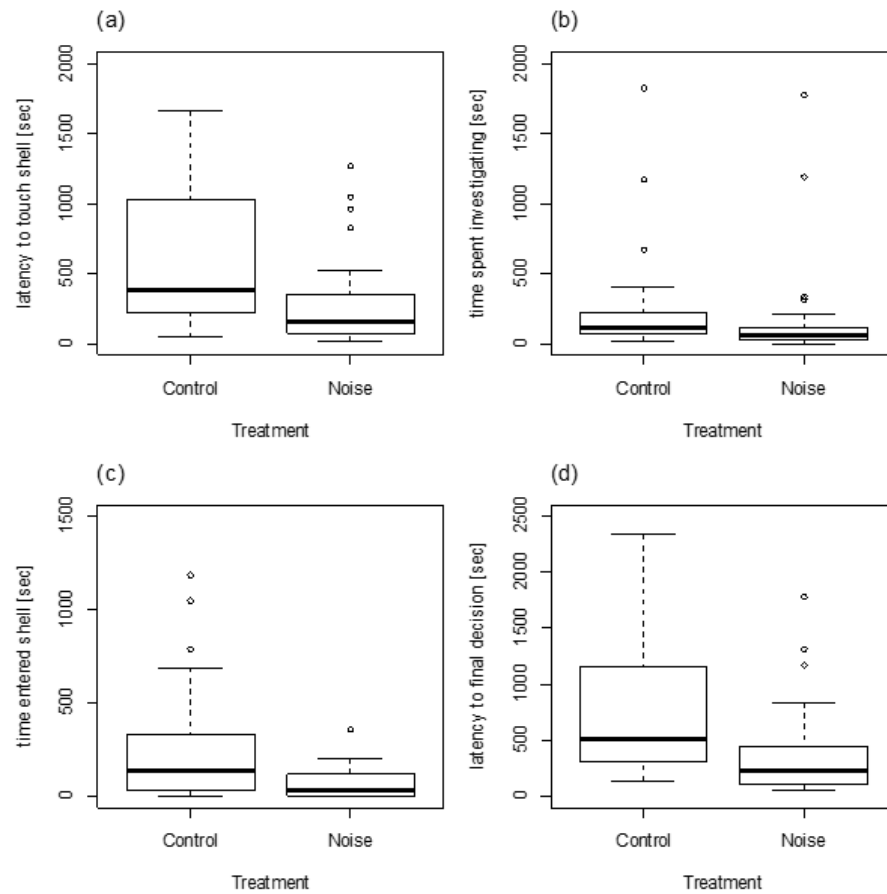
176 Competing interests. The authors declare no competing interests.

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181

**Figure 1.** The effect of noise on resource assessment in hermit crabs at different stages of shell selection (median and interquartile range): (a) latency to touch the preferred shell, (b) time spent investigating preferred shell, (c) time entered preferred shell and (d) latency to final decision.



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268 Electronic supplementary material

269 **Noise affects resource assessment in an invertebrate**

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271

272 Study species and holding conditions

273 Hermit crabs (*P. bernhardus*) were collected from rock pools in Ballywalter, Northern  
274 Ireland between December 2015 and February 2016. At this time of the year crab sex ratios  
275 are heavily biased towards females [1], therefore we only used females. For details on  
276 holding conditions see e.g. [2, 3]. Crabs were removed unharmed from their shells using a  
277 bench-vice, sexed, weighed, and assessed for missing limbs and parasites; damaged, or  
278 parasitized individuals were excluded e.g. [2, 4]. 24 hours before the experiment, each crab  
279 was individually isolated with an allocated shell in a plastic container filled with aerated  
280 seawater. To ensure standardised high levels of motivation across individuals to choose a  
281 better shell, crabs were given a non-preferred *Gibbula cineraria* shell, 50% the weight of  
282 each individual's relative ideal shell weight [1].

283

284 Playback protocol

285 The experiment consisted of one of two 30-minute treatments: anthropogenic noise,  
286 consisting of white noise cf. [5], or a control, consisting of a silent track, to rule out any effect  
287 of the speaker [6-8]. Stimuli were generated in Avisoft-SASLab Pro 5.1.17 (Avisoft  
288 Bioacoustics, Berlin, Germany) as WAV files (sample frequency 44.1 kHz, resolution 16 bit).  
289 Stimuli were played through a Denon PMA-720AE Amplifier, wired to an AQ SUB-AQUA



30 Underwater Speaker, suspended in the middle of the water column in the centre of the  
arena. As the majority of acoustic energy from anthropogenic sources occurs at low  
frequencies [9], white noise files were filtered above 2kHz (to reduce the output resonance of  
the speaker), which is well above *P. bernhardus*' hearing threshold [10] and played at ~165  
dB re 1 v/ $\mu$ Pa. Decibel levels were measured at several locations throughout the arena using a  
calibrated hydrophone with preamplifier (HTI-96-MIN; manufacturers calibrated sensitivity  
−165 dB re 1 v/ $\mu$ Pa; frequency range 2 Hz–30 kHz), connected to a Marantz PMD660  
recorder (44.1 kHz sampling rate; 0.3 Vrms input sensitivity), and calibrated using a signal of  
known amplitude [cf. [5], figure S1].

We chose white noise and not noise of actual pollutants, e.g. ship noise or pile-driving  
noise, as real world sounds of pollutants cannot be realistically reproduced using playback  
experiments e.g. [11, 12]. Moreover, the main focus of our work was to test how changes in  
the acoustic environment per se affect shell selection in hermit crabs.

Hermit crab shell selection behaviour is a widely studied and documented process  
which follows a series of distinct steps (e.g. [1, 13, 14]. In brief, different aspects of the  
focal shell are being assessed at different stages and prospective shells are initially identified  
visually. Shells are then approached and contacted with the antennae, which may provide  
chemical and tactile cues. These cues are then used to gain further information about the size,  
condition, weight, and both internal and external dimensions of the shell. As each step of the  
shell investigation process is completed, the amount of information gathered increases. Thus,  
individuals make a series of discrete decisions at each stage of the assessment process, i.e.  
continue investigating shell, accept shell, or reject shell. Therefore, to get a holistic

314 understanding regarding how changes in the acoustic environment affect resource  
315 assessment, each of the stages outlined below have to be included.

316

317         Here, we briefly describe the rationale why each of these measures was included (cf.  
318 [1, 13, 14]: (i) latency to contact shell (sec), which quantifies the time taken from the start of  
319 the experiment until an individual makes contact with the 100% shell; (ii) investigation (sec),  
320 which quantifies the duration between first contacting the shell and the point at which the  
321 crab makes a decision to either move into the 100% shell, or abandon all further shell  
322 investigation; (iii) latency to enter shell (sec), which is the length of time from the beginning  
323 of the experiment to the point at which the decision is made to leave the 50% shell and enter  
324 the 100% shell. Only crabs which moved into the 100% shell were included in this measure;  
325 (iv) final decision (yes/no), which quantifies whether the focal crab chooses to accept or reject  
326 the 100% shell. This is defined as the moment at which the crab stops investigating the other  
327 shell and moves away from the investigation site; and (v) latency to final decision (sec),  
328 which is the time taken from the beginning of the experiment to the point at which the crab  
329 moves away from the investigation site in its chosen shell. A crab may choose to swap shells  
330 several times after its first evacuation of the 50% shell.

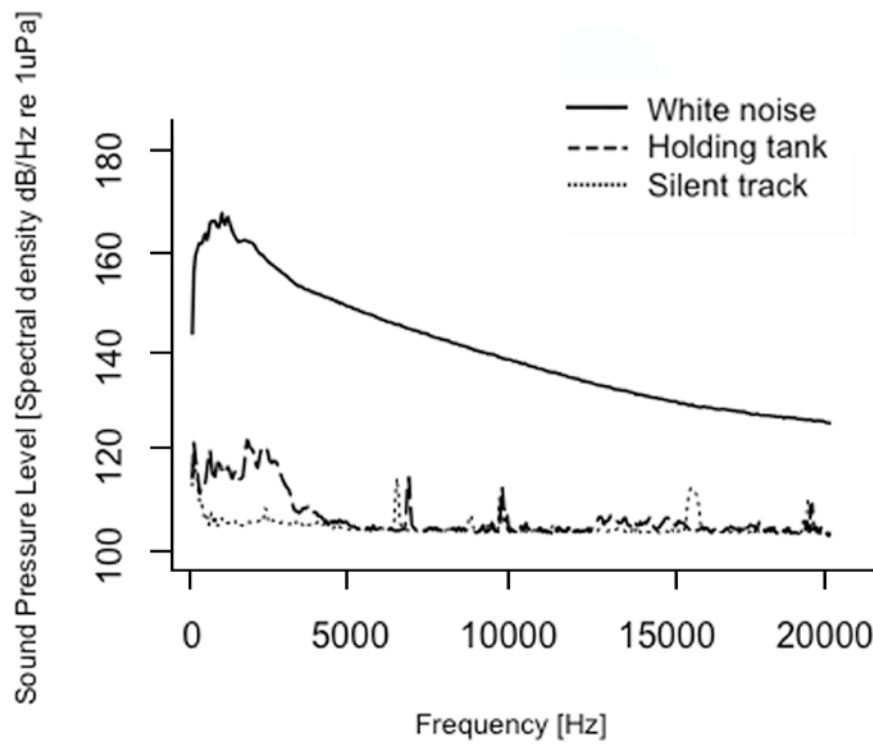
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332         Thus, “latency to enter shell” and “latency to final decision” reflect two different  
333 decision points. The first measure, entering the shell, quantifies the initial point at which the  
334 investigating individual decides to move into the new shell to further investigate it internally.  
335 However, it is common for crabs to reinvestigate the shell it has recently evacuated.  
336 Therefore, crabs may then swap back into the original shell, reinvestigate the new one, and/or  
337 may further swap between the shells. Hence, the point at which the final decision is made is

338 reached when the crab relinquishes investigation of any shell and moves away from the  
339 investigation site.

340

341           We designed the experiment in accordance with the reduction principle of the 3Rs  
342 [15]. To minimise the impact on individuals caused by handling and shell removal, each crab  
343 was exposed to only one treatment. After completion of experiments, all crabs were given a  
344 preferred shell and returned to the sea.



345

346 Figure S1. Averaged power spectra for anthropogenic noise (white noise), the control (silent),  
 347 and the ambient noise in the tank (fast Fourier transform size 1.024; Hann evaluation window;  
 348 spectrum level units normalized to 1 Hz bandwidth; 50% overlap; averaged from 5sec  
 349 recordings).

350

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